

REVIEW

How can calibrated research-based models be improved for use as a tool in identifying genes controlling crop tolerance to environmental stresses in the era of genomics—from an experimentalist's perspective

M.A. El-SHARKAWY*

Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia

Abstract

Almost four decades have passed since the new field of ecosystem simulation sprang into full force as an added tool for a sound research in an ever-advancing scientific front. The enormous advances and new discoveries that recently took place in the field of molecular biology and basic genetics added more effective tools, have strengthened and increased the efficiency of science outputs in various areas, particularly in basic biological sciences. Now, we are entering into a more promising stage in science, *i.e.* 'post-genomics', where both simulation modelling and molecular biology tools are integral parts of experimental research in agricultural sciences. I briefly review the history of simulation of crop/environment systems in the light of advances in molecular biology, and most importantly the essential role of experimental research in developing and constructing more meaningful and effective models and technologies. Such anticipated technologies are expected to lead into better management of natural resources in relation to crop communities in particular and plant ecosystems in general, that might enhance productivity faster. Emphasis is placed on developing new technologies to improve agricultural productivity under stressful environments and to ensure sustainable economic development. The latter is essential since available natural resources, particularly land and water, are increasingly limiting.

Additional key words: acclimation; adaptation; cassava; climate; CO₂; evapotranspiration; genomics; leaves; photosynthesis; productivity; respiration; soil; water; yield.

Introduction

To be able to feed the world in the coming 50–100 years (Sasson 1990), a concerted effort based on sound national agricultural policies, well-planned research strategies, and efficient delivery systems is a fundamental need (Buringh 1977, Wortman and Cummings 1978). Further, such integrated effort becomes more urgent in the face of global climate change and the associated many constraints limiting optimization of agricultural productivity worldwide (Hawksworth 1984, Desai 1986, Buxton *et al.* 1993). In particular, many countries in Africa, Asia, Middle East, and Latin America are currently experiencing an acute shortage of water due to both over-

consumption by increasing human populations and recurrent and prolonged drought (Brown 2002 http://www.greatlakesdirectory.org/zarticles/080902_water_shortages.htm). As the big gaps between potential and actual productivity have been largely closed in temperate zones agriculture, most future increases in agricultural production will probably come from developing countries, particularly in the tropics and subtropics where actual yields are still low due to several biotic and abiotic stresses. In this case, there is a crucial role for biotechnology and genomics in identifying gene(s) controlling tolerance to stresses and in breeding or engineering more

Received 25 November 2004, *accepted* 10 February 2005.

*Retired scientist; *present address:* A.A. 26360, Cali, Valle, Colombia; fax: (57-2) 442 1727, e-mail: elsharkawy@telesat.com.co

Acknowledgement: The author wishes to express his sincere appreciation for the unfailing encouragement and for the many valuable ideas, discussions, and inputs he received from Drs. J.D. Hesketh and M.G. Huck of USDA/ARS, University of Illinois at Urbana, USA and from his many former colleagues and co-workers at CIAT, Colombia during the development of this paper. The reprints and unpublished information received from various sources were also appreciated and acknowledged. Useful comments had been received from Dr. Douglas Laing, Cali, Colombia, and Dr. Mary Beth Kirkham, Kansas State Univ., Manhattan, KS, USA, and an anonymous reviewer. The computer's expertise of the young and energetic daughter Farah El-Sharkawy Navarro was instrumental in searching the net for crucial information and in retyping for many rounds this paper.

efficient and better adapted new crop cultivars. To enhance achievement of such a goal, a complementary role in the areas of molecular biology, interdisciplinary-oriented agricultural research, and crop modelling is warranted taking into account the paramount importance of testing new technologies under representative field conditions. Aided with relevant and integrative crop growth simulation models across a range of plant organization levels, interdisciplinary agricultural research should continue to play a pivotal role in generating useful and applicable technologies that are needed to enhance agricultural productivity, particularly in developing countries (Penning de Vries *et al.* 1989). This paper is a brief review of the

Justifications for simulating cropping systems

Previous justifications for crop modelling, analogous with Forresters's (1961) approach for industrial systems simulation in general and enhanced by computer's power availability in particular, are still viable. A good one can be found on the DOE website providing human genome project information: <http://doegenomestolife.org/program/goal4.shtml>: to 'Develop the computational methods and capabilities to advance understanding of complex biological systems and predict their behaviour'. We need to understand better how plant processes interact, particularly under stresses, to control plant growth and yield. We need to find critical plant structural, biochemical, and molecular biology of enzymes, and physiological traits and associated genes, which if improved will result in higher yields (Hermans and Westhoff 1990, Raghavendra *et al.* 2003). These objectives have been with us for some time. Recent emphasis on post-genomics only makes this goal more urgent.

Over the past 40 years considerable resources have gone into studying and modelling photosynthetic processes from biochemistry to canopy (see Boote and Loomis 1991). In the light of recent successes in plant genetic engineering (see Collins and Shepherd 1996), it may soon be possible to select for or bioengineer leaves with superior biochemical photosynthetic potential to take advantage of higher than normal atmospheric CO₂ (Raghavendra *et al.* 2003). We have known for some time that leaf area is important, based upon the Leaf Area Index (LAI): Net Assimilation Rate (NAR) models, which are based mainly on data and a few simple

history of simulation efforts in more than 40 years, with emphasis on what should be done better for developing research-based crop models in order to improve its utility and applicability into the real world of cropping systems. Thus, the aims and scope of this paper are to outline the weakness and strength in the current efforts of crop modelling considering that details of theories and concepts underlying model buildings, along with the biological processes/environments involved, had been previously dealt with in details in many books and reviews (see *e.g.* Loomis *et al.* 1979, Whisler *et al.* 1986, Penning de Vries *et al.* 1989, Hodges 1991, Boote and Loomis 1991, Amthor 2000).

calculations (Watson 1947, 1952, Muramoto *et al.* 1965). Leaf or LAI behaviour is not being studied in the same detail as biochemical photosynthetic processes. Plant breeders and agronomists have selected for a greater partitioning of dry matter toward economic yield (*i.e.* greater harvest indices, HI) and optimal LAI values for crop production among genotypes and plant populations (row widths, plant densities) exposed to a range of ecosystem environments (see Evans 1993), which have resulted in Nobel and the Japan Prizes (for the so-called 'Green Revolution' dwarf cereals research). However, most of this research was conducted in absence of major production constraints and the high yielding new cultivars required large capital and intensive agrichemical production inputs in order to maximize productivity. One of the most remarkable outcomes of the 'Green Revolution' technology was the substantial increase in food production that was badly needed in many developing countries (Sasson 1990). Nevertheless, vast world agricultural areas are characterized by various degrees of biotic and abiotic stresses that limit productivity, warrant development of new technologies through breeding and selection for tolerance to a wide range of stresses, particularly under field conditions with low production inputs, such as in cassava (Nickel 1987, El-Sharkawy and Cock 1987b, El-Sharkawy *et al.* 1990, Hershey and Jennings 1992, El-Sharkawy 1993, 2003, Pellet and El-Sharkawy 1993a,b, 1997, DeTafur *et al.* 1997a,b, El-Sharkawy and Cadavid 2000, 2002), and in many other crops (see Buxton *et al.* 1993).

Responses to stress: acclimation vs. adaptation

Musgrave and his students (Baker and Musgrave 1964) studied maize photosynthesis in the field in the middle 1950's. That work stimulated a revolution in our understanding of how photosynthesis, respiration, and transpiration of field-acclimated plants behave. Improvements in instrumentation by the *LI-COR* company helped this revolution prosper *via* its pioneering technologies. These were two remarkable achievements rarely acknowledged.

Japanese scientists (cited in El-Sharkawy and Hesketh 1964, El-Sharkawy *et al.* 1965, 1967, 1968, Muramoto *et al.* 1965) also had been working in the field for some time on photosynthesis of rice. We early recognized the importance of germ-plasm-based physiological and agronomical research under field conditions as in cotton (El-Sharkawy *et al.* 1965, Muramoto *et al.* 1965), cereals (El-Sharkawy 1975), and cassava (Kawano *et al.* 1978,

1998, Cock *et al.* 1979, Connor and Cock 1981, Connor *et al.* 1981, Veltkamp 1985, El-Sharkawy and Cock 1987b, Cock and El-Sharkawy 1988, El-Sharkawy 1990, 1993, 2003, El-Sharkawy *et al.* 1990, 1998, Hershey and Jennings 1992, Pellet and El-Sharkawy 1993a,b, 1997, DeTafur *et al.* 1997a,b, El-Sharkawy and Cadavid 2000, 2002). All of these efforts have led to a better characterization of varietal and genotypic performances under different environments, and elucidation of mechanisms underlying productivity and tolerance to stresses and the identification of useful plant traits for breeding and selection for better adapted and high yielding new cultivars. Furthermore, these research efforts provided essential data for developing effective and experimentally-based crop simulation models.

Before discussing how a crop model handles 'responses to stress' we need to note that 'acclimate' is defined to describe form and functional adjustments to short-term stress brought on by changes in climate, environment, or other circumstances. 'Adapt' is often defined the same way, but botanists reserve it for long-term genetic adjustments to the stress factors. It gets very confusing when both terms apply to what is going on in the same system. Some successful experimental ecologists deliberately use the term 'adapt' for short term responses to stress, it being a somewhat less clever word. The experimentalist-modeller should be wary when encountering 'adapt' or 'adaptation' as some scientists, especially those of British school, get very upset about their misuse. This focus on the use of these two words has occurred during some very important breakthroughs in photosynthesis and transpiration research, with terminology papers published at the same time, aimed at undermining credit for pioneering agronomic C₃:C₄ photosynthesis research and modelling innovations on how to study plant-water relations (Gaastra 1959, El-Sharkawy and Hesketh 1965, El-Sharkawy *et al.* 1967, 1968, Šesták *et al.* 1971).

Stress acclimation has been a problem in physiological research; a potted plant inadvertently allowed to stress severely because of improper watering often does not re-acclimate to normal conditions before elaborate stress studies are made (automatic irrigation partially solved the problem). Potted plants grown in shade at the same time further inflate the problem (see Boardman 1977); all of this resulted in leaves energy-saturated at low irradiances with low photosynthetic and transpiration rates prior to the early 1960's, with a few exceptions (see El-Sharkawy and Hesketh 1986).

We have continually pointed out test-plant 'acclimation' problems that have slowed scientific progress from the early 1960s on, such as in studies of photosynthetic rate constants and irradiance response curves in various crop species (El-Sharkawy and Hesketh 1964, El-Sharkawy *et al.* 1965, 1968, 1990, 1992a, 1993), studies of the cassava C₃:C₄ intermediates (Cock *et al.* 1987, El-Sharkawy and Cock 1987a, CIAT 1990–95), and of temperature effects on cassava leaf area

development, crop growth and yield (Irikura *et al.* 1979) and photosynthetic rate constants of cassava in response to water stress, irradiance, air humidity, temperature, and CO₂ (El-Sharkawy and Cock 1984, 1990, El-Sharkawy *et al.* 1984, 1992a, 1993, CIAT 1990–95, Cayón *et al.* 1997). Observed characteristics of leaf anatomy, high leaf photosynthetic rates, no photon saturation up to 1 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, high optimal temperature for photosynthesis, 30–40 °C, low photorespiration, high % of labelled ¹⁴C in initial products of C₄ acids, and elevated activities of the C₄ enzyme phosphoenolpyruvate carboxylase (PEPC) in leaves of cultivated cassava and wild *Manihot* species grown under intense sunlight and hot-dry climates might indicate that these species represent an example of a C₃:C₄ intermediate (Cock *et al.* 1987, El-Sharkawy and Cock 1987a, 1990, CIAT 1992–95, Tenjo *et al.* 1993, El-Sharkawy *et al.* 1992a, El-Sharkawy 2003, 2004). Under prolonged water stress in the field, in intense sunlight and high air temperatures, the activities of PEPC in cassava leaves increased or remained unchanged, as compared to those in well-watered plants, while those of the C₃ enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) were greatly reduced (CIAT 1992, 1993, Lopez *et al.* 1993, El-Sharkawy 2003, 2004). In such leaves, leaf photosynthesis rates were significantly correlated with PEPC activities (El-Sharkawy 2003, 2004). Moreover, in a wide range of cassava germplasm grown under field conditions in humid, seasonally dry and semiarid environments, total biomass and storage root yield were significantly correlated with upper canopy leaf photosynthetic rates as measured in the field (CIAT 1990, 1992, 1993, El-Sharkawy and Cock 1990, El-Sharkawy *et al.* 1990, 1993, Pellet and El-Sharkawy 1993a, DeTafur *et al.* 1997b). In the main, the relation was due to non-stomatal factors (*i.e.* biochemical/anatomical factors). The storage root yield was also significantly correlated with intercellular CO₂ concentration (negatively) and with leaf photosynthetic nitrogen use efficiency (LPNUE = leaf photosynthetic rate per unit of total leaf N) (El-Sharkawy *et al.* 1990, CIAT 1993, DeTafur *et al.* 1997b, El-Sharkawy 2003, 2004), thus emphasizing the role of activities of photosynthetic enzymes. Cassava lacks leaf Kranz anatomy (El-Sharkawy and Cock 1987a, 1990) typical of higher plant C₄ leaves, which is essential for the separation and compartmentalization of the C₃ and C₄ main enzymes (El-Sharkawy and Hesketh 1965, Laetsch 1974, Hatch 1977, El-Sharkawy and Hesketh 1986). From an evolutionary point of view it is possible that cassava and its wild relatives are midway in their biochemical evolution towards C₄ photosynthesis. Species in the family Euphorbiaceae have CAM, C₃, or C₄ pathways and apparently also intermediates. Cassava plants grown in well-lit growth cabinets, probably with high atmospheric humidity, did not show the intermediate behaviour, which adds another dimension to this C₄ evolutionary theory (Edwards *et al.* 1990, Ueno and Agaric 1997).

Controlled environment plants have helped studying photosynthetic responses to temperature and provided temperature functions for crop models (see Berry and Björkman 1980); data from different elevations and latitudes as reported by Irikura *et al.* (1979), CIAT (1992–95), El-Sharkawy and Cock (1990), and El-Sharkawy *et al.* (1992a, 1993) offer a good calibration for controlled-environment data, if not a better source of information for modelling. Researchers using controlled environments should calibrate their plants against some plants growing outside. Sometimes a farmer will point out that controlled-environment plants look bad, when in fact if they pulled up a single plant from one of their own densely-planted fields they might be amazed at how unhealthy such plants often look.

This acclimation problem for trying to predict how field-grown plants can behave under full sunlight using data on plants grown under controlled environments still confuses scientists, when a few simple calibration experiments on field- and controlled environment-grown plants would solve the problem. Evans (1993) discussed the various aspects involved in environmental adaptation of crop growth and yield as well as the physiological processes underlying crop improvement. Boardman (1977) reviewed plant's adaptation to light and the comparative photosynthesis of sun and shade plants. Kasperbauer (1999) and Kasperbauer *et al.* (1986, 1998) studied the effects of quality of photons on growth, yield, and photosynthate allocation among different plant organs in various crops grown in the field using plant residual and coloured-plastic mulches. Osaki *et al.* (2004) modelled the role of node unit in photosynthate distribution. Thornley (1998, 2002, 2004) developed a theoretical model that accounts for leaf photosynthetic acclimation to light and N limitations and for the relative contribution of sun and shade leaves to crop canopy photosynthesis. Šesták (1985) documented research on leaf development, structure, function, and physiology as adapted to environmental factors. Nevertheless, recent research on plant responses to elevated CO₂ (EC) under controlled conditions, in open-top chambers and in FACE (free-air CO₂ enrichment)-conducted experiments with herbaceous and woody species have revealed some useful information about possible causes underlying photosynthetic acclimation. The term 'photosynthetic down-regulation' commonly used in literature refers to only one facet of acclimation, *i.e.* reduction in the rates and capacity of the photosynthetic process. The observed photosynthetic down-regulation had been attributed to one or more of the following factors: a decrease in stomatal conductance to gas diffusion, imbalance in source/sink ratio for photosynthate within the whole plant system, feedback inhibition of photosynthesis due to soluble saccharide accumulation in leaves, decreases in photosynthetic biochemical capacity (including both light and dark reactions), and lesser leaf content of RuBPCO (Chen *et al.* 1993, 1995a,b, Xu *et al.* 1994, Rogers *et al.* 1998, Dickson

et al. 2000, Adam *et al.* 2004, Bunce and Sicher 2004). In other cases, the long-term exposure to EC did not result in reduction in photosynthesis.

Sholtis *et al.* (2004) reported that in a FACE experiments within an established sweet-gum (*Liquidambar styraciflua*) closed-canopy forests there was a long-term positive response to EC without apparent reduction in photosynthetic capacity. Moreover, these authors provided an informative mini-review on photosynthetic acclimation. Also, Hesketh *et al.* (1984), Radin *et al.* (1987), Hileman *et al.* (1994), and Begonia *et al.* (1986b, 1987, 1996, 1999) found small or no significant reduction in stomatal conductance while leaf photosynthesis was significantly enhanced in cotton grown in EC as compared to rates in plants grown in ambient air. Sharma-Natu *et al.* (2004), working with mung bean grown in field at atmospheric CO₂ concentration (AC) and EC inside open-top chambers for the entire period of growth found no down-regulation in leaf photosynthesis and in one cultivar there was enhancement. Bunce and Sicher (2004) found no photosynthetic down-regulation in kohlrabi plants grown in EC due to its large stems acting as sink for excess saccharides while collards, lacking large stems, showed down-regulation whose extent depended on the irradiance used. Thus the observed photosynthetic down-regulation in collards was associated with glucose and fructose contents than with sucrose or starch. Feedback inhibition of photosynthesis, due to accumulation of glucose and fructose, was apparently the underlying cause for down-regulation in this case. Ziska *et al.* (1991) reported about 56 % increase in leaf photosynthesis of cassava grown in EC under controlled conditions (at 300 cm³ m⁻³ above AC) indicating absence of down-regulation. Moreover, Fernández *et al.* (2002), in an open-top chamber experiments, found that EC (at 680 cm³ m⁻³) enhanced cassava leaf photosynthesis compared to those in plants grown in AC. The absence of photosynthetic down-regulation in cassava grown in EC was apparently associated with greater carboxylation efficiency of RuBPCO despite reductions in soluble protein and N contents in leaves. Also, leaf contents of soluble sugars and starch decreased in plants grown in EC suggesting strong sinks for photosynthates as indicated by increases in both shoot and storage roots' biomass. These findings imply that cassava productivity, as a source for food, feed, and energy in the tropics and subtropics, is likely to be enhanced by the expected increases in AC and associated rises in global temperature. Cassava photosynthesis (El-Sharkawy and Cock 1984, 1990, El-Sharkawy *et al.* 1984, 1992a, 1993, Ramanujam 1990, CIAT 1992–95) and yield and growth (Irikura *et al.* 1979, Connor *et al.* 1981, Keating *et al.* 1982, Fukai *et al.* 1984, CIAT 1992–95, El-Sharkawy *et al.* 1990, 1992b, 1993, 1998, Ramanujam 1990, El-Sharkawy 1993, 2003, 2004, Pellet and El-Sharkawy 1993a, 1997, El-Sharkawy and Cadavid 2000, 2002) were greatest in tropical and subtropical environments in

wetter soils and with higher temperature, air humidity, and intense sunlight.

History of cropping systems' models and related ongoing research

Knowing the evolution of crop modelling to date is helpful for determining how to proceed with the above objective (see for example, Penning de Vries *et al.* 1974, 1989, Penning de Vries 1975, Loomis *et al.* 1979, Bunce 1986, Whisler *et al.* 1986, Thornley and Johnson 1990, Boote and Loomis 1991, Hodges 1991, Peart and Curry 1997). Recently, several review and assessment papers discussed the underlying theory and conceptual basis, the application, validity, and utility of empirical/descriptive and mechanistic/explanatory crop simulation models developed over 30 years (Boote *et al.* 1983, Swaney *et al.* 1983, Fye *et al.* 1984, Mishoe *et al.* 1984, Shorter *et al.* 1991, Baker 1996, Boote *et al.* 1996, Monteith 1996, Passioura 1996, Sinclair and Seligman 1996, Poluektov and Topaj 2001). Empirical or functional models rely on a few simple mathematical equations or algorithms with little attention to the underlying mechanisms while describing crop growth, phenotypic and genotypic variations, and responses to complex environments. The simplified forms of these empirical models are well-illustrated by the statistically-based multiple regression-models and by those describing the functional components of crop growth, yield, and their responses to environments (see Hanks and Rasmussen 1982, Penning de Vries *et al.* 1989, Hodges 1991, Shorter *et al.* 1991). On the other hand, the mechanistic models are based on dynamic rate concepts and are constructed using many detailed algorithms describing in quantitative manner events, biological processes and mechanisms, as affected by environments, at various plant levels that may range from enzymes to crop canopy (see Whisler *et al.* 1986, Boote and Loomis 1991, Hodges 1991). The empirical crop models are easy to apply, given the modest information and inputs required for their application, and are useful and more widely used for management purposes than the mechanistic ones. The mechanistic or explanatory models, however, are useful as research tools, used mainly by its builders, for better understanding the complex biological processes in plants/communities and in analyzing the plant-environment interactions (see Boote *et al.* 1983, Ritchie and Johnson 1990). In few cases it is used to predict crop performance under new environments and climates where the crop has never been grown before and for assessing the impact of breeding and selection programs on cultivar variations for specific traits (Penning de Vries *et al.* 1989), as well as in evaluating alternative cropping system's management (Ng and Loomis 1984, Mishoe *et al.* 1984). In general, there is more pessimism concerning the effectiveness and utility of simulation crop models, particularly the comprehensive ones. However, the effectiveness of a simulation model in achieving its objective depends largely on the balance between the theory and its associated assumptions underlying model's

development and what is going on in the real world. Thus, the more the model is built on sound experimental research with enough supporting data and with less ambiguity in its structure the more effective and valid it is in simulating processes, and in predicting performances actually occurring in plant ecosystems and crop communities. Unless this calibration to field conditions is undertaken, modellers often fail in achieving their objectives in their simulation (see Fye *et al.* 1984). There are papers of Cock *et al.* (1979), El-Sharkawy and Cock (1987b), Cock and El-Sharkawy (1988), and El-Sharkawy (2003, 2004) on cassava ideotype under both favourable and stressful environments, the Reddy *et al.* (1997) leaf/internode paper, Zhang *et al.* (2001) phenology paper, the Pan MSc. and Ph.D. theses (1997, 2000) and Pan *et al.* (2000) phenology/dry matter paper backing up the Pan crop model, as well as a new Chinese field research paper on photoperiodism in soybeans (Han *et al.* unpublished).

The experimentalists involved, directly or indirectly, in evolving crop models know how weak the logic and scientific literature is in backing up those models. Also they know how fast the tax money can be wasted trying to correct the problem. Hence we need much more thought on how to proceed.

The early British work on leaf area development (LA), leaf area index (LAI), crop growth rate (CGR), and net assimilation rate (NAR) (Watson 1947, 1952), the extensive work on leaf development and photosynthetic behaviour (see Šesták 1985), and the papers of Monsi and Saeki (1953) and Saeki (1960) on crop irradiance interception and canopy photosynthesis laid a foundation for crop modelling. However, there were different views concerning who was the first among the British and the Japanese workers in initiating crop modelling (see Sinclair and Seligman 1996, Poluektov and Topaj 2001). Gaastra (1959) came up with an innovative leaf photosynthesis-transpiration model based upon the physical principles of gas fluxes in and out of the leaf. His model was supported by careful research and was later used in software development by the *LI-COR* company and by many other companies in Europe and Japan for manufacturing portable infrared gas analysers, which can be used to calculate leaf gas exchange flux rate constants. Moreover, El-Sharkawy and Hesketh (1965) and El-Sharkawy *et al.* (1967) extended and applied Gaastra's leaf gas exchange model in their research on photosynthesis and transpiration in C₄ and C₃ species. Penning de Vries *et al.* (1974, 1989) and Penning de Vries (1975) estimated and added up the respiration energy requirements for the synthesis of various organic substances such as proteins, fats, starch, and cellulose as well as carbon costs for synthesis and maintenance within plant cells and tissues based on details of biochemical

pathways involved and by building on the equation of McCree (1974) for estimating the rate of growth and maintenance respiration in white clover and grain sorghum. Also, MacDermitt and Loomis (1981) added more insight by quantitatively assessing the elemental composition of plant biomass in relation to its energy contents, growth efficiency, and productivity. All these efforts have led to more progress in crop modelling and to very detailed studies on plant respiration and on its implications for overall crop productivity (see Evans 1993, Amthor 2000).

While computers were used in the kinds of modelling cited above, another critical paper in US plant modelling efforts is that of Duncan *et al.* (1967). Duncan (a retired Kentucky maize farmer) did the computer modelling and Hanau provided the needed data set. By using the relation between different arrangements in leaf canopies and sunlight profile within canopy, this model was able to describe canopies with maximum use of sunlight. It also explored effects of saccharide stresses on plant growth. At about the same time in the Netherlands, another critical, but static, model on photosynthesis of leaf canopy was elaborated by de Wit (1965) which laid the basis for further development of more comprehensive series of dynamic explanatory models at Wageningen. Ritchie *et al.* (for recent versions, see 1985a,b) did a water budget model based upon evapotranspiration models (for a comprehensive treatment of the concept of crop evapotranspiration and its practical application in various crops see Allen *et al.* 1998) where he separated plant transpiration from soil evaporation by applying a photon interception : LAI relationship. This model is probably the most effective experimentally-based simulation effort used to date with wide application for plant-water-soil relation analysis (Ritchie and Johnson 1990), in contrast to the numerous theoretical ones with little supporting experimental data. Singh (1999), while building on Ritchie's model, discussed the essential field data needed for soil water balance simulation in semiarid environments, hence emphasizing the importance of more collaboration needed between modellers and experimentalists. Begonia *et al.* (1986a,b) were involved in an irrigation experiment in Starkville, Mississippi, using rain-protected plots. The soil was heavy and deep, with big cracks when dried out. Plants given no water, a medium amount of water and ample water produced plants and leaves that were small, medium, and large with little observable wilting as well as associated small, medium, and large final yields. Un-watered plants over a sand lens in the soil profile went into a severe wilt early on and remained that way until the crop matured. Obviously there are soil and atmospheric conditions where leaves will wilt, such as large plants exposed to severe water stress. Pettigrew (2004a,b) saw severe wilting in cotton field studies on light soils in Stoneville, Mississippi. Models must be able to predict both kinds of behaviour. Connor *et al.* (1981), Porto (1983), Cock *et al.* (1985), El-Sharkawy and Cock

(1987b), CIAT (1992, 1993, 1994), El-Sharkawy *et al.* (1992b), El-Sharkawy (1993), Cayón *et al.* (1997), De Tafur *et al.* (1997a,b), and El-Sharkawy and Cadavid (2002) studied extended water stress effects on cassava in the field and saw varying degrees of moderate wilting but leaves remained photosynthetically active throughout stress due to partial stomatal closure in response to edaphic and atmospheric water deficits as well as deeper rooting, hence preventing severe leaf dehydration (*i.e.* stress avoidance mechanisms).

Duncan (1973) and D.N. Baker combined the Davis model with Ritchie's model as available in the early 1970's, as well as with other data at Starkville, Mississippi, on cotton to produce SIMCOT, which explored interactions between saccharide and water stress effects on growth and yield. There was a wealth of canopy photosynthetic, respiration, and morphogenetic data at Starkville from which McKinion and Jones *et al.* (1974) developed logic to greatly improve the model, resulting in SIMCOT II.

Jones *et al.* (1974) added the soil/crop nitrogen budget to SIMCOT II, the latter needed by insect modellers (his associated modified and differently named SIMCOT II cotton model was described in these publications). Pierce Jones (personal communication), working on his Ph.D. with J.W. Jones at the University of Florida created an internet agricultural extension service, collaborating with agricultural extension people at the location. Zhang *et al.* (2002) added to the internet agricultural extension efforts with software for storing past crop performance and related weather data. Some of this work may not seem particularly sophisticated, but what was important was its timing and its impact on agriculture production systems. It should have been done a decade earlier as progress begets progress. This work was needed to bridge the gap between crop simulation models at the time and a practical application. It led to better N : P205 : K20 budgets in the model. The Florida and Ritchie's groups, and others (see Hoogenboom *et al.* 1992, White *et al.* 1995) using their models developed the first generic crop simulation models. Moreover, White and Hoogenboom (1996) described and evaluated the GeneGro model, which is a version of the dry bean model BEANGRO V1.01, incorporating effects of several genes influencing physiological traits such as phenology, growth habit, and seed size. They concluded that for certain plant traits few genes must be characterized to accurately simulate cultivar differences, and pointed to the potential for developing similar models to study the effects of genes in relation to plant adaptation in other crops. Mathews (1998) reported the first elaborate P205 model for a cassava ecosystem (not yet supported by research). His model was part of a cassava general ecosystem model, built in the cotton model tradition (Matthews and Hunt 1994), supported by research from the CIAT (Irikura *et al.* 1979, Connor *et al.* 1981, El-Sharkawy and Cock 1984, 1987b, 1990, El-Sharkawy *et al.* 1984, 1990, 1992a,b, 1993,

1998, Veltkamp 1985, El-Sharkawy 1993, Pellet and El-Sharkawy 1993a,b, 1994, 1997, DeTafur *et al.* 1997a,b, El-Sharkawy and Cadavid 2002). Gray (2000) reported on another cassava model.

The group at Mississippi State University (McKinion *et al.* 1975, 1989, Baker *et al.* 1983, Fye *et al.* 1984) also added US soil taxonomic information and soil-water physical theory to their GOSSYM/COMAX cotton model. Wang *et al.* (1986) emphasized the role of holes and cracks in the profile on water flow and root distribution. Bowman *et al.* (1994, 2003) reviewed the problem and found considerable water flowing down through a dry block of a soil profile in cracks and pores. Soil taxonomists knew about the problem all along but were somewhat intimidated by soil physicists from talking about it. A prominent soil physicist at University of California, Davis discovered the problem when testing his model in the field but covered it up, although he talked about it at scientific meetings. Soil physical-chemical models for water and nutrient behaviour near soil particle surfaces were developed by others for predicting the flow of pollutants through a soil profile. Others are also now working on models for soil formation to predict cracks, holes, and hardpans (fragipans) as well as other soil types. One might easily envision complicated probability theory to describe holes, cracks, hardpans, and crusting; coefficients needed in the theory may be a bit hard to come by. El-Sharkawy (1975), working in the Libyan Sahara Desert, was faced with a stratified sandy soil profile with a fine sandy hardpan that stopped root

growth but not water flow further down the profile. Field plant scientists including modellers need under-graduate level reviews from soil taxonomists describing similar problems.

The state of the art of such models can be seen in abstracts given at global change symposium at Reading University (see Ingram *et al.* 1999). Kawano *et al.* (1978, 1998), Veltkamp (1985), El-Sharkawy and Cock (1987b, 1990), Cock and El-Sharkawy (1988), El-Sharkawy *et al.* (1990, 1992b, 1998), CIAT (1992–95), El-Sharkawy (1993, 2003), Pellet and El-Sharkawy (1993a,b, 1997), DeTafur *et al.* (1997a,b), and El-Sharkawy and Cadavid (2000, 2002) took the plant ideotype approach, searching for form and function traits that might lead to higher yields. This effort, of course, lays the groundwork for post-genomic studies of how plant processes and their interactions in a crop simulation model are controlled by genes or gene function (Fregene *et al.* 2001, Akano *et al.* 2002, Fregene and Puonti-Kaerlas 2002, Okogbenin and Fregene 2002). The definition of a gene is now in a flux.

The use of computer technology in genomic and post-genomic studies has been described at the DOE 'Human Genome Project Information' website. One example is the work of Ware *et al.* (2002) who developed the Gramene software at Cold Spring Harbor, NY. Pan *et al.* (2000 and personal communication) recently has reported on more much needed genomic software; their contributions to bioinformatics and comparative genomics are incredible, all of which came after their crop modelling research.

What remains to be done better

Detailed interactive process models to understand and quantify effects of stresses on crop performance are required before others can determine associated gene function. The computer power is in superabundance and is thus not a limiting factor. Studies are needed on root systems, phenology, and growth dynamics under stresses, using 'calibrated' (this means digging up fine root systems and getting dry matter and root distribution, see Böhm 1979, Connor *et al.* 1981, Aresta and Fukai 1984, El-Sharkawy and Cock 1987b, Pellet and El-Sharkawy 1993b, Tscherning *et al.* 1995, El-Sharkawy 2004) minirhizotrons, particularly in rain-protected plots (see Begonia *et al.* 1986a,b) or in the field, both with irrigated and non-irrigated plots, for different soil types (Pettigrew 2004a,b). Water and N stresses need to be quantified for plant shoots at the same time with emphasis on photosynthetic acclimation problems to N, water, and irradiance limitations (see Boardman 1977, Thornley 1998, 2002, 2004). All such large scale studies need elaborate phenological and dry matter measurements for vegetative and reproductive growth (Pan 1997). These techniques need to be employed in (modified) FACE experiments. Crop simulation modelling as a means of integrating logic from new and old results is critical to the success of such large

scale efforts, else they are a waste of tax payer's money. Apparently the CERES-wheat model (Ritchie 1985, Ritchie *et al.* 1985a,b) was tested at the wheat Arizona FACE experimental site.

Experimentalists need to do a better job of quantifying stresses occurring during their experiments. In order to do this, it is important that plant scientists understand the budgeting or book keeping methods used in the models to account for saccharides, water, and other nutrients (N, P, K): income is compared to costs (supply vs. growth demands) for each morphological unit in the plant (phytomers, reproductive organs, and roots) and growth decisions are made accordingly (see Hodges 1991, Baker and Davies 1995, Thornley 1998). Such morphological units at maturity require some or relatively little supply, like a mature fruit or stem. If demand is greater than supply, then decisions must be made to slow shoot growth, eliminate growing plant parts, or grow more roots. Priorities must be set for which organs are supplied. Rules are set up to make such decisions. It is important now to understand the various structural and functional plant responses to environmental stresses such as water shortage (see Kreeb *et al.* 1989) and the role of growth regulators and other physiological mechanisms

(see Davies *et al.* 1986, Kutáček *et al.* 1990, Baker and Davies 1995, Alves and Setter 2000, 2004) involved in this decision-making process. At any moment in time we need to understand the genetic controls for behaviour of dividing cells in the plant, realizing that much of the plant has mature or dead cells. Also we need to understand processes involved in leaf area production, development, and its dynamics and functions in relation to crop productivity under stresses (Connor and Cock 1981, Porto 1983, Fukai *et al.* 1984, Šesták 1985, Evans 1993, Pellet and El-Sharkawy 1993a, 1997, DeTafur *et al.* 1997a, El-Sharkawy and Cadavid 2002, Cowling and Field 2003, Alves and Setter 2004) and the role of hormones such as abscisic acid (Davies *et al.* 1986, Kutáček *et al.* 1990, Alves and Setter 2000) and abscission of leaves and fruits (Baker and Davies 1995). The plant needs to be broken down into phytomers, tissues (cambium), stems, and fruits or fruit parts and roots. The British Growth Analysis method with its LA, LAI, dry mass (M), and dM/dt , dA/dt is no longer of much help by itself and must be integrated with McCree (1974) equation for estimating respiration and with Monsi and Saeki (1953) and Röhrig *et al.* (1999) within crop canopies light interception models to provide useful software if possible. Modellers must test their rules and priorities against what plants do in the real world under similar stresses. Of course, if supply exceeds demand, reserves can build up as in the case of some results obtained in EC experiments. More information is needed on whole plant photosynthate reserve capacity, alternative sinks, saccharides' sink-source relation, partitioning dynamics of photosynthate and essential mineral nutrients, and the mechanisms of feedback controls on photosynthesis as affected by stresses (Neales and Incoll 1968, Bunce 1986, El-Sharkawy 1993, 2003, 2004, Pellet and El-Sharkawy 1994, Xu *et al.* 1994, Cayón *et al.* 1997, De Tafur *et al.* 1997a, Rogers *et al.* 1998, Dickson *et al.* 2000, Fernández *et al.* 2002, Bunce and Sicher 2004).

While much research during the past 50 years had been devoted to photosynthetic biochemical, biophysical,

and carbon processing mechanisms, leaf behaviour and associated stresses are equally important if not more involved (see Šesták 1985). For leaf growth, emphasis should be on leaf primordia, small leaf (1 cm), fully expanded leaf, and dead leaf appearance rates up the main stem *vs.* physiological time (degree days), to define leaf senescence effects; physiological measurements should be made at different leaf ages (see Šesták 1985, Evans 1993). The same goes for internode primordia, small internode (1 cm), and fully extended internode events *vs.* physiological time, to give leaf position in the canopy. Equations for leaf/internode dimensional changes and dry matter/N accumulation complete the model. Reddy *et al.* (1997) have already done some of this for cotton. Plant's stages of growth in expensive field experiments need to be defined based upon elaborate measurements such as these. How much further one goes to get leaf angles, *etc.* or how much further detail the model needs is open to argument. Details of plant canopies and their structure, form, and function as essential components in crop simulation are discussed by Russel *et al.* (1989). Thornley (1998, 2002, 2004) is close to creating software enabling experimentalists to use the Monsi-Saeki equation along with crop measurements given above as well as actual measurements of light interception within the canopy to predict canopy photosynthesis from actual leaf photosynthetic measurements. These could be combined with respiration models and associated measurements to give a more complete picture. Such software would be similar to the Gaastra equations available for some time accompanying photosynthetic equipment from private suppliers.

Portis and Salvucci (2002) described how the enzyme RuBPCO activase was discovered and subsequently researched, leaving out management details. Their history is very relevant to understanding how discoveries are made; more of this is needed. We do need cases illustrating when management went astray during such dramatic discovery events.

Ongoing problems in maintaining productivity in multidisciplinary teams

Before we proceed with the question we must mention the recent Discover interview by Jocelyn Salem (2004) with Lord Robert May who advocated allowing young people to pursue their own agenda and express their creativity; somehow this must be done within the framework of a goal a multidisciplinary team is working on. He implies it can not be done; teamwork entices the 'plodders'. We have seen many examples of where it can be done, but often by ignoring management's close direction. One should read his entire interview where he, for example, ranked both Switzerland and United Kingdom higher than USA with respect to research management styles as well as scientific productivity per capita.

The DOE 'Human Genome Project Information'

website emphasizes the importance of team research. Natural and agricultural ecosystems are so complex that large multidisciplinary teams are needed to effectively solve associated research problems. Shorter *et al.* (1991) discussed the complementary roles needed among plant breeders, plant physiologists, and crop modellers in order to enhance the process of crop improvement and their genotypic adaptation to diverse environments.

For searching related information about management theory available on the internet, key words like 'managing conflicts in work teams', 'developing disciplinary teams', and 'establishing and nurturing research collaboration' bring up some relevant information. Also there are books and papers on research management to be

consulted. For example, John Nickel (1989), while building on his long career as a research manager in international agricultural research systems in developing countries, discussed in detail problems encountered in multidisciplinary teams, challenges in planning, and execution of strategies underlying better management, and means to make research more efficient. His book makes an interesting reading for any young researcher who aspires to be a future manager for agricultural research institutions, particularly in developing countries.

Modern management theory for team research decrees that those in a team inclined to steal what someone else has done be immediately transferred out or terminated; this, of course, includes the team's manager. Also there are now effective group methods [democratic political procedures or futures (stock market) betting games] for determining what research to do, how to divide up the resources, and who to collaborate with or hire. There were some past examples of misbehaviour within team efforts we knew about, but human nature being what it is and with some especially rank recent behaviour, it is pointless to take up space here citing examples. Instead we will discuss some general principles:

(1) Any member of a team making a scientific contribution to the effort should receive full credit for what he/she did, as well as associated financial rewards. Graduate students and post-docs will happily settle for first authorship on associated publications. Their author-

ship rights, still being abused because their vulnerability in the job market, must be protected. Other team members, including the manager, should be cautious about subsequent review papers, meeting presentations, and books discussing what a team member did.

(2) Team members with the potential for making a big contribution should get financial backing needed, within budgetary limits.

(3) Non-scientists, by definition not using the experimental method, need to focus on how to solve scientific problems and not on how to steal credit for what someone else has done. The scientific method can be used effectively to challenge someone else's reported work. While it is part of the system to do so without new experiments, if one turns out to be wrong in such a challenge, he/she should be penalized.

(4) Scientists who have the courage to speak out their minds and freely express their views and concerns about poor research management and obvious abuses must not be intimidated and their careers should not be threatened. To the contrary, they should be encouraged and commended for their stance. The views of such scientists must be taken seriously into consideration in order to remedy deficiencies and eliminate abuses in the system that would certainly reflect positively upon science quality and reputation as well as on its efficiency in delivering required outputs.

The cost : benefit ratio of ecosystem modelling and associated research

Computer science, which has revolutionized our workplace, was mainly developed by nerds with notoriously little leadership ability, although many found ways to make money when the opportunity rose. We need to emphasize more the important role of nerds and mavericks in our society among our young people and to stop encouraging incompetent management/leadership or rewarding it so much in the workplace.

To minimize cost and time, for example, this paper was written and edited using PC's, not a secretary or assistants as usual. Drafts of the paper were distributed among interested colleagues across countries over the internet; sometimes the discussions got a little heated with repeated editions in view of new and relevant information. New literature was searched using the internet, which proved very effective; sources often supplied even better information, which we cited. One merely has to type in critical key words; often reprints of the papers were available. References were easily obtained using a search tool. The young reader is aware of all this, to a retired scientist this capability seems amazing. Even at the library, a PC can be used the same way to locate sources. Garfield (1992) has single-handedly replaced the scientific society award system for outstanding research, with his 'citation classics' (prior to 1992) or now his 'citation laureates', based upon some criteria and a com-

puter analysis of citation scores listed by published papers in peer reviewed journals. Of course once one understands this new system, there are ways to game it to become an 'outstanding scientist', replacing the politics once needed in the scientific society award system. All the above is leading rapidly to a revolution in agricultural extension, university teaching, libraries, and the need for congregating large numbers of people in cities (which now presents a large potential security threat). It also has brought what once was considered outlying research laboratories into the mainstream, as recently proven by discoveries made in such laboratories.

Ecological modelling has finally made natural ecosystem and crop ecology respectable sciences, when used to integrate literature and new research results. Earlier the emphasis was on classification systems, as well as sampling methods, without much synthesis.

One needs to ask in any cost-benefit analysis what was discovered and what is the potential for a discovery that might benefit mankind? We list innovations in crop modelling in the history given above; progress was slow but steady.

The plant ecosystem models in effect represent a major advance in photosynthetic research, with emphasis on effects of stresses and leaf dynamics, particularly leaf senescence in relation to irradiance and N limitations,

among other stresses (Thornley 1998, 2002, 2004). Eco-system modelling should continue as long as photosynthetic research exists; photosynthetic scientists should make an effort to contribute to it. We need large multidisciplinary experiments where the phenology and structure of the crop as well as the form and function of its parts are properly defined. Some time ago large expensive experiments were run where the plots were undisturbed, using aerodynamic techniques to measure gas and energy exchange. Possibly better crop evapotranspiration models were developed but the knowledge base in crop physiology remained undisturbed. One wonders what was discovered by the sophisticated and very expensive FACE experiments; numerous interesting findings have been reported using open-top chambers (see papers by Chen *et al.* 1993, 1995a,b, Begonia *et al.* 1996, 1999, Bunce and Sicher 2004, Sharma-Natu 2004) such as stomatal acclimation (present and absent), responses to drought, leaf starch and sugar contents, photosynthesis feedback inhibition mechanisms, *etc.* One needs to be hesitant before putting out large expensive but media attractive experiments. Well supported large multidisciplinary teams need to be in place with broad stress-related experiments to ensure that something useful comes out from such experiments.

The best place to do water stress research is in the desert under irrigation, as is the best place to put controlled environment facilities (greenhouses). Techniques used in Starkville, MS, should have been used in the desert (generally one does not need rain-protected plots there and plants in well-built greenhouses there look more like field-grown plants).

There is a faction of experimentalists closely associated with the modelling effort that was frustrated in the past by the multidisciplinary problems encountered in the teams involved. Nevertheless, these experimentalists made major contributions to logic used in the models. Sometimes the models were used to analyze data from complex field experiments on stress; a good example is the work of Caverio *et al.* (2000); this approach needs to be used more in the future in order to increase research efficiency. Irikura *et al.* (1979), El-Sharkawy and Cock (1990), El-Sharkawy *et al.* (1990, 1992a, 1993), and CIAT (1992–95) did research at different elevations and latitudes in the tropics to get at temperature effects on cassava growth, yield, and photosynthesis responses, thus obviating the need for expensive phytotrons or growth cabinets. Han *et al.* (unpublished) report on photoperiod studies done in the field and four locations at different latitudes (photoperiod was controlled by dark chambers and latitude). In both experiments weather and soil variations are a factor, but using field-grown experimental material overrides this criticism. One needs to study these papers; the use of models for interpreting their data sets might be quite effective.

Aerodynamic measurements of photosynthesis and CO₂ field release experiments did not disturb the eco-

system much but also generally did not lead to significant discoveries. Here the cost/benefit ratio was very high. Open-top chamber CO₂ releases at Phoenix, Arizona controlled environment greenhouse studies led to exceptional leaf sugar and starch contents, with mottling of leaves because of back-reflection of radiation by the starch grains (see Chen *et al.* 1993, 1995a). This was a major discovery but unfortunately has not been exploited to study associated stress effects on photosynthesis and translocation. Obviously, starch and sugars build up will occur when saccharide supply is exceptional and demand is low. It is pointless to comment on what was found in the Phoenix experiments without doing analysis of the materials, balance of one's experimental system and quantifying stress effects on saccharide supply and demand.

The plant respiration equation (McCree 1974, Amthor 2000) was derived from the British Growth Analysis equations. Old animal science books on preparing nutritional feeds for animals contain huge tables on cellulose, soluble saccharides, proteins, and fats (see for example Cuthbertson 1969) and the old biochemistry books give how much sugar it takes to synthesize these products. One does not need elaborate theoretical models to calculate respiratory costs but then one should not ignore their results if available (Amthor 2000). Maintenance respiration costs need a theoretical estimate, but scientific measurements might be better, although experimental techniques for measuring both maintenance and growth respiration are difficult to deploy. In Amthor's (2000) review, one table revealed that the theoretical studies were cited 200–300 times while the one experiment was cited 80 times.

There is a 'snake oil' factor in crop modelling (see Passioura 1996). The Duncan *et al.* (1967) and El-Sharkawy and Hesketh (1965) citation classics illustrate this syndrome. The former represented a small advance in synthesizing what goes on in a complex ecosystem, using a very sophisticated data set that was perfect of the modelling effort, while the latter represented an agronomic pioneering effort reporting critical studies of the C₃:C₄ phenomenon and called attention to earlier work on C₄ acid products in sugarcane leaves carried out at the Hawaii Sugarcane Plantation (Kortschak *et al.* 1965). This latter was also a major discovery (though an earlier Russian paper by Yuri Karpilov in 1960, which went unnoticed for some time by photosynthesis researchers in English speaking countries, reported on the presence of C₄ acid products in maize leaves); both pioneering works led to many subsequent papers (see Hatch and Slack 1966, Hatch 1977). We report above on discoveries made during the modelling work; the C₃:C₄ discoveries were in another league. Yet the modelling work was cited more times; it often dwarfed the C₃:C₄ work at scientific meetings and in textbooks. The early C₄:C₃ leaf photosynthesis and transpiration work (El-Sharkawy and Hesketh 1965, El-Sharkawy *et al.* 1967) did rely,

however, on the Gaastra's model equations (1959).

We make a case for using detailed models to identify genes controlling complex processes, but if an experimentalist understands the logic that underlies these models he might greatly simplify how to identify such genes (see *e.g.*, White and Hoogenboom 1996); what now seems complex will become obvious. And, of course, it is far more efficient to just do the research (with emphasis on molecular behaviour at the gene level), keeping the modelling logic in mind. And doing research on modelling logic can be exciting, leading to discoveries. Wang *et al.*'s soils hole and crack paper (1986) decimated years of expensive highly theoretical soil physics modelling; soils research had to be reoriented towards modelling soil formation processes leading to holes, cracks, surface crusts, and hardpans. In their studies, roots were found growing in the holes and cracks, modifying assumptions made earlier in root models. Leaf senescence is an important factor in predicting leaf photosynthesis (Thornley 1998, 2002). We have pointed out the needed phenological and structural plant measurements needed to specify leaf age, size, and place in the canopy over time. The molecular factors and genetics underlying leaf senescence is now being studied in detail in the laboratory and field (Biswal and Biswal 2000 <http://www.ias.ac.in/currsci/sep25/articles19.htm>, Behera

et al. 2003, Raghavendra *et al.* 2003) some controlling genes had been identified and isolated; one only has to search the critical words (*e.g.* Biswal and Biswal 2000).

Money managers need to ask scientists what the cost/benefit ratio is for what they plan to do, and crop modelling is very expensive. We need to find ways for experimentalists to collaborate with computer scientists, using existing resources. It might be appropriate if more crop modellers like Pan (see Ware *et al.* 2002) and Brendel *et al.* (2004) became involved in bioinformatics.

The cost/benefit ratio is about as good as the ratio of computer scientists to experimentalists involved. It also is as good as the ratio of the cost of scientific management to the cost of active scientists using the scientific method and who must deliver outputs from their research efforts. Moreover, it pays to remember that private companies gave us: (1) the hardware and software to implement Gaastra's model for leaf gas exchange plus many other useful instruments, (2) the human genome discovery in a record time, (3) the biochemical details of C₄ pathway, (4) the bioengineered plants, which increase yields and reduce pesticide use and environmental pollution. Public-funded scientists at universities and at national and international research laboratories, and particularly theoretical modellers, might set their sights on these outstanding achievements.

Summary

Besides the need that scientists should be ever more diligent in citing relevant earlier research and giving credits to where it originally belongs, also needed are: (1) Textbooks and manuals for experimentalists on logic needed for quantitative plant ecosystem models, aimed at undergraduates or experimentalists in other disciplines. Publications such as those by Allen *et al.* (1998), Singh (1999), Biswal and Biswal (2000 <http://www.ias.ac.in/currsci/sep25/articles19.htm>), and Bowman and Reynolds (2003) are good examples for the type of interdisciplinary reviews needed for undergraduate teaching and for experimentalists in other disciplines. (2) Better management methods for nurturing multidisciplinary team collaboration and 'genius' when it appears and for enforcing zero toleration of interdisciplinary snobbish attitudes. Rules for authorship should be established in the case of modelling and related research; the current situation particularly in the US is disgraceful. Programmers could claim first authorship on their software, experimentalists on the logic and its data base. Software should not undergo minor manipulations and be renamed and claimed by

others without giving credit to the original work. (3) More research on water stress, root behaviour, soil pores, cracks, crusts, and hard pans, leaf saccharide feed back control on photosynthesis, and leaf behaviour (senescence) as affected by irradiance, nitrogen, and other limitations. However, all growth cabinet users must be aware that irradiance acclimation was supposed to be eliminated as a research problem some 50 years ago. (4) More emphasis on the scientific method. (5) Better overall multidisciplinary team management methods. Clearly, there is a need for a system where young people can challenge old ideas and get away with it – they should not be suppressed or intimidated for challenging the past. Salaries for innovative scientists should be greatly enhanced, in comparison to those for management, with emphasis on their individual discoveries. National and international scientific awards should be conferred on those innovative scientists but not on politicians. Scientists deliberately need to find ways to collaborate with scientists in other disciplines, if only for innovative ideas that come from such interactions.

References

- Adam, N.R., Wall, G.W., Kimball, B.A., Idso, S.B., Webber, A.N.: Photosynthetic down-regulation over long-term CO₂ enrichment in leaves of sour orange (*Citrus aurantium*) trees. – *New Phytol.* **163**: 341-347, 2004.
- Akano, A.O., Dixon, A.G.O., Mba, C., Barrera, E., Fregene, M.: Genetic mapping of a dominant gene conferring resistance to cassava mosaic disease. – *Theor. appl. Genet.* **105**: 521-525, 2002.

- Allen, R.G., Pereira, L.S., Raes, D., Smith, M.: Crop evapotranspiration – Guidelines for computing crop water requirements – FAO Irrigation and drainage paper 56. FAO, Rome 1998.
- Alves, A.A.C., Setter, T.L.: Response of cassava to water deficit: leaf area growth and abscisic acid. – *Crop Sci.* **40**:131-137, 2000.
- Alves, A.A.C., Setter, T.L.: Response of cassava leaf area expansion to water deficit: cell proliferation, cell expansion and delayed development. – *Ann. Bot.* **94**: 605-613, 2004.
- Amthor, J.S.: The McCree-deWit-Penning de Vries-Thornley respiration paradigms: 30 years later. – *Ann. Bot.* **86**: 1-20, 2000.
- Aresta, R.B., Fukai, S.: Effects of solar radiation on growth of cassava (*Manihot esculenta* Crantz). II. Fibrous root length. – *Field Crops Res.* **9**: 361-371, 1984.
- Baker, D.N., Lambert, J.R., McKinion, J.M.: GOSSYM: a simulator of cotton growth and yield. – *South Carolina Agr. Exp. Stat. Tech. Bull.* 1983.
- Baker, D.N., Musgrave, R.B.: Photosynthesis under field conditions. V. Further plant chamber studies of the effects of light on corn (*Zea mays* L.). – *Crop Sci.* **2**: 127-131, 1964.
- Baker, J.M.: Use and abuse of crop simulation models: foreword. – *Agron. J.* **88**: 689, 1996.
- Baker, N.R., Davies, W.J.: Control of Plant Growth. – Cambridge Univ. Press, Cambridge 1995.
- Begonia, G.B., Begonia, M.F.T., Ousby, B.R., Johnson, M.: Vegetative and reproductive responses of cotton to state-specific CO₂ enrichment and drought stress. – *J. Mississippi Acad. Sci.* **44**: 190-196, 1999.
- Begonia, G.B., Hesketh, J.D., Hodges, H.F.: Effects of long-term drought and nitrogen on fruiting and yield of cotton. – In: Nelson, T.C. (ed.): Proc. Beltwide Cotton Prod. Res. Conf. Pp. 71-75. Nat. Cotton Council of America, Memphis 1986a.
- Begonia, G.B., Hesketh, J.D., Pettigrew, W.T., Peters, D.B.: Cotton leaf photosynthesis in enriched CO₂. – In: Nelson, T.C. (ed.): Proc. Beltwide Cotton Prod. Res. Conf. Pp. 76-77. Nat. Cotton Council of America, Memphis 1986b.
- Begonia, G.B., Hesketh, J.D., Woolley, J.T., Peters, D.B.: Variability in leaf photosynthetic CO₂ exchange rates near saturating irradiance and CO₂. – *Photosynthetica* **21**: 584-587, 1987.
- Begonia, G.B., Russ, B., Cunningham, S.G., Moore, R.: Evidence of not photosynthetic acclimation to cotton exposed to state-specific CO₂ enrichment. – *J. Mississippi Acad. Sci.* **41**: 95-98, 1996.
- Behera, S.K., Nayak, L., Biswal, B.: Senescing leaves possess potential for stress adaptation: the developing leaves acclimated to high light exhibit increased tolerance to osmotic stress during senescence. – *J. Plant Physiol.* **160**: 125-131, 2003.
- Berry, J., Björkman, O.: Photosynthetic response and adaptation to temperature in higher plants. – *Annu. Rev. Plant Physiol.* **31**: 491-543, 1980.
- Boardman, N.K.: Comparative photosynthesis of sun and shade plants. – *Annu. Rev. Plant Physiol.* **28**: 355-377, 1977.
- Böhm, W.: Methods of Studying Root Systems. – Springer-Verlag, Berlin 1979.
- Boote, K.J., Jones, J.W., Mishoe, J.W., Berger, R.D.: Coupling pests to crop growth simulators to predict yield reduction. – *Phytopathology* **73**: 1581-1587, 1983.
- Boote, K.J., Jones, J.W., Pickering, N.B.: Potential uses and limitations of crop models. – *Agron. J.* **88**: 704-716, 1996.
- Boote, K.J., Loomis, R.S. (ed.): Modeling Crop Photosynthesis – from Biochemistry to Canopy. – Crop Science Society of America and American Society of Agronomy, Madison 1991.
- Bowman, B.T., Brunke, R.R., Reynolds, W.G., Wall, G.J.: Rainfall simulator grid lysimeter system for solute transport studies using large intact soil blocks. – *J. Environ. Quality* **23**: 815-822, 1994.
- Bowman, B.T., Reynolds, W.D.: FAQ-Water Flow in Soils. – Southern Crop Protection and Food Res. Ctr., London 2003.
- Brendel, B., Pan, X., Sparks, M.E.: Bioinformatics: The interpretation of genomic information. – In: Brummer, C., Wilson, R.F. (ed.): Legume Crop Genomics. Pp. 256-267. Amer. Oil Chem. Soc., Champaign 2004.
- Bunce, J.A.: Measurements and modeling of photosynthesis in field crops. – *CRC crit. Rev. Plant Sci.* **4**: 47-77, 1986.
- Bunce, J.A., Sicher, R.C., Jr.: Daily irradiance and feedback inhibition of photosynthesis of elevated carbon dioxide in *Brassica oleracea*. – *Photosynth. Res.* **41**: 481-488, 2004.
- Buringh, P.: Food production potential of the world. – *World Development* **5**: 477-485, 1977.
- Buxton, D.R., Shibles, R., Forsberg, R.A., Blad, B.L., Asay, K.H., Paulsen, G.M., Wilson, R.F. (ed.): International Crop Science I. – Crop Science Society of America, Madison 1993.
- Cavero, J., Farre, I., Debaeke, P., Faci, J.M.: Simulation of maize yield under water stress with the EPICphase and CROPWAT models. – *Agron. J.* **92**: 679-690, 2000.
- Cayón, M.G., El-Sharkawy, M.A., Cadavid, L.F.: Leaf gas exchange of cassava as affected by quality of planting material and water stress. – *Photosynthetica* **34**: 409-418, 1997.
- Chen, X.M., Alm, D.M., Hesketh, J.D.: Effects of atmospheric CO₂ concentration on photosynthetic performance of C3 and C4 plants. – *Biotronics* **24**: 65-72, 1995a.
- Chen, X.M., Begonia, G.B., Alm, D.M., Hesketh, J.D.: Responses of soybean leaf photosynthesis to CO₂ and drought. – *Photosynthetica* **29**: 447-454, 1993.
- Chen, X.M., Begonia, G.B., Hesketh, J.D.: Soybean stomatal acclimation to long-term exposure to CO₂ enriched atmospheres. – *Photosynthetica* **31**: 51-57, 1995b.
- CIAT: Cassava Program Annual Report for 1990 (1992, 1993, 1994, 1995). – Centro Internacional de Agricultura Tropical, Cali 1990 (1992, 1993, 1994, 1995).
- Cock, J.H., El-Sharkawy, M.A.: Physiological characteristics for cassava selection. – *Exp. Agr.* **24**: 443-448, 1988.
- Cock, J.H., Franklin, D., Sandoval, G., Juri, P.: The ideal cassava plant for maximum yield. – *Crop Sci.* **19**: 271-279, 1979.
- Cock, J.H., Porto, M.C.M., El-Sharkawy, M.A.: Water use efficiency of cassava. III. Influence of air humidity and water stress on gas exchange of field grown cassava. – *Crop Sci.* **25**: 265-272, 1985.
- Cock, J.H., Riaño, N.M., El-Sharkawy, M.A., López, Y., Bastidas, G.: C₃-C₄ intermediate photosynthetic characteristics of cassava (*Manihot esculenta* Crantz). II. Initial products of ¹⁴CO₂ fixation. – *Photosynth. Res.* **12**: 237-241, 1987.
- Collins, G.B., Shepherd, R.J. (ed.): Engineering Plants for Commercial Products and Applications. – New York Academy of Sciences, New York 1996.
- Connor, D.J., Cock, J.H.: Response of cassava to water shortage. II. Canopy dynamics. – *Field Crops Res.* **4**: 285-296, 1981.
- Cowling, S.A., Field, C.B.: Environmental control of leaf area production: implications for vegetation and land-surface modeling. – *Global Biogeochem. Cycles* **17**: doi:10.1029/2002GB001915, 2003.

- Cuthbertson, D. (ed.): Assessment of and Factors Affecting Requirements of Farm Livestock. – Pergamon Press, Oxford 1969.
- Davies, W.J., Metcalfe, J., Lodge, T.A., da Costa, A.R.: Plant growth substances and the regulation of growth under drought. – *Aust. J. Plant Physiol.* **13**: 105-125, 1986.
- de Tafur, S.M., El-Sharkawy, M.A., Cadavid, L.F.: Response of cassava (*Manihot esculenta* Crantz) to water stress and fertilization. – *Photosynthetica* **34**: 233-239, 1997a.
- de Tafur, S. M., El-Sharkawy, M.A., Calle, F.: Photosynthesis and yield performance of cassava in seasonally dry and semi-arid environments. – *Photosynthetica* **33**: 229-257, 1997b.
- Desai, P.: Weather and Grain Yields in the Soviet Union. – International Food Policy Research Institute, Washington 1986.
- de Wit, C.T.: Photosynthesis of leaf canopies. – *Agr. Res. Rep. (Pudoc-Wageningen)* **663**: 1-57, 1965.
- Dickson, R.E., Tomlinson, P., Isbrands, J.G.: Partitioning of current photosynthate to different chemical fractions in leaves, stems, and roots of northern red oak seedlings during episode growth. – *Can. J. Forest Res.* **30**: 1308-1317, 2000.
- Duncan, W.G.: SIMCOT: A simulation of cotton growth and yield. – In: Murphy, C., Hesketh, J.D., Strain, B. (ed.): *Modelling the Growth of Trees*. Pp. 115-118. Oak Ridge Nat. Lab., Oak Ridge 1973.
- Duncan, W.G., Loomis, R.S., Williams, W.A., Hanau, R.: A model for simulating photosynthesis in plant communities. – *Hilgardia* **38**: 181-205, 1967.
- Edwards, G.E., Sheta, E., Moore, B. de, Dai, Z., Fransceschi, V.R., Cheng, S.-H., Lin, C.-H., Ku, M.S.B.: Photosynthetic characteristics of cassava (*Manihot esculenta* Crantz), a C₃ species with chlorenchymatous bundle sheath cells. – *Plant Cell Physiol.* **31**: 1199-1206, 1990.
- El-Sharkawy, M.A.: Crop Research in Kufra Oasis, Libya. – Agric. Dev. Council, Tripoli 1975.
- El-Sharkawy, M.A.: Effect of humidity and wind on leaf conductance of field grown cassava. – *Rev. bras. Fisiol. veg.* **2**: 17-22, 1990.
- El-Sharkawy, M.A.: Drought-tolerant cassava for Africa, Asia and Latin America: breeding projects work to stabilize productivity without increasing pressures on limited natural resources. – *BioScience* **43**: 441-451, 1993.
- El-Sharkawy, M.A.: Cassava biology and physiology. – *Plant mol. Biol.* **53**: 241-261, 2003.
- El-Sharkawy, M.A.: Cassava biology and physiology. – *Plant mol. Biol.* **56**: 481-501, 2004.
- El-Sharkawy, M.A., Cadavid, L.F.: Genetic variation within cassava germplasm in response to potassium. – *Exp. Agr.* **36**: 323-334, 2000.
- El-Sharkawy, M.A., Cadavid, L.F.: Response of cassava to prolonged water stress imposed at different stages of growth. – *Exp. Agr.* **38**: 333-350, 2002.
- El-Sharkawy, M.A., Cadavid, L.F., de Tafur, S.M.: Nutrient use efficiency of cassava differs with genotype architecture. – *Acta agron. Univ. Nacional-Palmira-Colombia* **48**: 23-32, 1998.
- El-Sharkawy, M.A., Cock, J.H.: Water use efficiency of cassava. I. Effects of air humidity and water stress on stomatal conductance and gas exchange. – *Crop Sci.* **24**: 297-502, 1984.
- El-Sharkawy, M.A., Cock, J.H.: C₃-C₄ intermediate photosynthetic characteristics of cassava (*Manihot esculenta* Crantz). I. Gas exchange. – *Photosynth. Res.* **12**: 219-235, 1987a.
- El-Sharkawy, M.A., Cock, J.H.: Response of cassava to water stress. – *Plant Soil* **100**: 345-360, 1987b.
- El-Sharkawy, M.A., Cock, J.H.: Photosynthesis of cassava (*Manihot esculenta*). – *Exp. Agr.* **26**: 325-340, 1990.
- El-Sharkawy, M.A., Cock, J.H., Held, K.A.A.: Water use efficiency of cassava. II. Differing sensitivity of stomata to air humidity in cassava and other warm-climate species. – *Crop Sci.* **24**: 503-507, 1984.
- El-Sharkawy, M.A., Cock, J.H., Lynam, J.K., Hernandez, A. del P., Cadavid, L., F.L.: Relationships between biomass, root-yield and single-leaf photosynthesis in field-grown cassava. – *Field Crops Res.* **25**: 183-201, 1990.
- El-Sharkawy, M.A., de Tafur, S.M., Cadavid, L.F.: Potential photosynthesis of cassava as affected by growth conditions. – *Crop Sci.* **32**: 1336-1342, 1992a.
- El-Sharkawy, M.A., de Tafur, S.M., Cadavid, L.F.: Photosynthesis of cassava and its relation to crop productivity. – *Photosynthetica* **28**: 431-438, 1993.
- El-Sharkawy, M.A., Hernandez, A. del P., Hershey, C.: Yield stability of cassava during prolonged mid-season water stress. – *Exp. Agr.* **28**: 165-174, 1992b.
- El-Sharkawy, M.A., Hesketh, J.D.: Effects of temperature and water deficit on leaf photosynthetic rates of different species. – *Crop Sci.* **4**: 514-518, 1964.
- El-Sharkawy, M., Hesketh, J.: Photosynthesis among species in relation to characteristics of leaf anatomy and CO₂ diffusion resistances. – *Crop Sci.* **5**: 517-521, 1965.
- El-Sharkawy, M.A., Hesketh, J.D.: Citation Classic – Photosynthesis among species in relation to characteristics of leaf anatomy and CO₂ diffusion resistances. – *Curr. Cont./Agr. Biol. Environ.* **27**: 14, 1986.
- El-Sharkawy, M., Hesketh, J., Muramoto, H.: Leaf photosynthetic rates and other growth characteristics among 26 species of *Gossypium*. – *Crop Sci.* **5**: 173-175, 1965.
- El-Sharkawy, M.A., Loomis, R.S., Williams, W.A.: Apparent reassimilation of respiratory carbon dioxide by different plant species. – *Physiol. Plant.* **20**: 171-186, 1967.
- El-Sharkawy, M.A., Loomis, R.S., Williams, W.A.: Photosynthetic and respiratory exchanges of carbon dioxide by leaves of the grain amaranth. – *J. appl. Ecol.* **5**: 243-251, 1968.
- Evans, L.T.: *Crop Evolution, Adaptation and Yield*. – Cambridge Univ. Press, Cambridge 1993.
- Fernández, M.D., Tezara, W., Rengifo, E., Herrera, A.: Lack of downregulation of photosynthesis in a tropical root crop, cassava, grown under an elevated CO₂ concentration. – *Funct. Plant Biol.* **29**: 805-814, 2002.
- Forrester, J.W.: *Industrial Dynamics*. – Massachusetts Inst. Technol. Press, Cambridge 1961.
- Fregene, M., Okogbenin, E., Mba, C., Angel, F., Suarez, M.C., Guitierrez, J., Chavarriaga, P., Roca, W., Bonierbale, M., Tohme, J.: Genome mapping in cassava improvement: challenges, achievements and opportunities. – *Euphytica* **120**: 159-165, 2001.
- Fregene, M., Puonti-Kaerlas, J.: Cassava biotechnology. – In: Hillocks, R.J., Thresh, J.M., Bellotti, A.C. (ed.): *Cassava: Biology, Production and Utilization*. Pp. 179-207. CABI Publishing, New York 2002.
- Fukai, S., Alcoy, A.B., Llamelo, A.B., Patterson, R.D.: Effects of solar radiation on growth of cassava (*Manihot esculenta* Crantz): I. Canopy development and dry matter growth. – *Field Crops Res.* **9**: 347-360, 1984.
- Fye, R.E., Reddy, V.R., Baker, D.N.: The validation of

- GOSSYM: Part 1-Arizona conditions. – *Agri. Syst.* **14**: 85-105, 1984.
- Gaastera, P.: Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusion resistance. – *Meded. Landbouwhogeschool (Wageningen)* **59**(13): 1-68, 1959.
- Garfield, E.: The effectiveness of American Society of Agronomy Journals: A citationist's perspective. – In: *Research Ethics, Manuscript Review and Journal Quality*. Pp. 1-13. ACS Misc. Publ., ISI, Pennsylvania 1992.
- Gray, V.M.: A comparison of two approaches for modelling cassava (*Manihot esculenta* Crantz) crop growth. – *Ann. Bot.* **85**: 77-99, 2000.
- Hanks, R.J., Rasmussen, V.P.: Predicting crop production as related to plant water stress. – *Adv. Agron.* **35**: 193-215, 1982.
- Hatch, M.D.: C₄ pathway photosynthesis: mechanism and physiological function. – *Trends biochem. Sci.* **2**: 199-202, 1977.
- Hatch, M.D., Slack, C.R.: Photosynthesis by sugar-cane leaves. A new carboxylation reaction and the pathway of sugar formation. – *Biochem. J.* **101**: 103-111, 1966.
- Hawthornth, D.L. (ed.): *Advancing Agricultural Production in Africa*. – Commonwealth Agricultural Bureaux, Farnham Royal 1984.
- Hermans, J., Westhoff, P.: Analysis of expression and evolutionary relationships of phosphoenolpyruvate carboxylase genes in *Falveria trinervia* (C4) and *F. pringlei* (C3). – *Mol. gen. Genet.* **224**: 459-468, 1990.
- Hershey, C.H., Jennings, D.L.: Progress in breeding cassava for adaptation to stress. – *Plant Breed. Abstr.* **62**: 823-831, 1992.
- Hesketh, J.D., Woolley, J.T., Peters, D.B.: Leaf photosynthetic CO₂ exchange rates in light and CO₂ enrichment rates in light and CO₂ enriched environments. – *Photosynthetica* **18**: 536-540, 1984.
- Hileman, D.R., Huluka, G., Kenjigel, P.K., Sinha, N., Bhattacharya, N.C., Biswas, P.K., Lewin, K.F., Nagy, J., Hendrey, G.R.: Canopy photosynthesis and transpiration of field-grown cotton exposed to free-air CO₂ enrichment (FACE) and differential irrigation. – *Agr. Forest Meteorol.* **70**: 189-207, 1994.
- Hodges, T. (ed.): *Predicting Crop Phenology* – CRC Press, Boca Raton 1991.
- Hoogenboom, G., Jones, J.W., Boote, K.J.: Modeling the growth, development and yield of grain yields using SOYGRO, PNUTGRO and BEANGRO: a review. – *Trans. ASAE* **35**: 2043-2056, 1992.
- Ingram, J., Sutton, K., Hunt, T.: GCTW Working Document 24, GCTW Focus 3 Cassava Network. Symposium Abstracts: Food and Forestry – Global Change and Global Challenges. The GCTE Focus 3 Conference 1999.
- Irikura, Y., Cock, J.H., Kawano, K.: The physiological basis of genotype-temperature interactions in cassava. – *Field Crops Res.* **2**: 227-239, 1979.
- Jones, J.W., Hesketh, J.D., Kamprath, E.J., Bowen, H.D.: Development of a nitrogen balance for cotton growth models. – *Crop Sci.* **14**: 541-546, 1974.
- Kasperbauer, M.J.: Cotton seedling root growth responses to light reflected to the shoots from straw-covered versus bare soil. – *Crop Sci.* **39**: 164-167, 1999.
- Kasperbauer, M.J., Hunt, P.G.: Far-red light affects photosynthate allocation and yield of tomato over red mulch. – *Crop Sci.* **38**: 970-974, 1998.
- Kasperbauer, M.J., Karlen, D.L.: Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. – *Physiol. Plant.* **66**: 159-163, 1986.
- Kawano, K., Daza, P., Amaya, A., Rios, M., Goncalves, W.M.F.: Evaluation of cassava germplasm for productivity. – *Crop Sci.* **18**: 377-380, 1978.
- Kawano, K., Narintaraporn, K., Narintaraporn, P., Sarakarn, S., Limsila, A., Limsila, J., Suparhan, D., Sarawat, V., Watananonta, W.: Yield improvement in a multistage breeding program for cassava. – *Crop Sci.* **38**: 325-332, 1998.
- Keating, B.A., Evenson, J.B., Fukai, S.: Environmental effects on growth and development of cassava (*Manihot esculenta* Crantz). I. Crop development. – *Field Crops Res.* **5**: 271-281, 1982.
- Kortchak, H.P., Hart, C.K., Burr, G.O.: Carbon dioxide fixation in sugarcane leaves. – *Plant Physiol.* **40**: 209-213, 1965.
- Kreeb, K.H., Richter, H., Hinckley, T.M. (ed.): *Structural and Functional Responses to Environmental Stresses: Water Shortage*. – SPB Academic Publ., The Hague 1989.
- Kutáček, M., Elliott, M.C., Macháček, I. (ed.): *Molecular Aspects of Hormonal Regulation of Plant Development*. – SPB Academic Publ., The Hague 1990.
- Laetsch, W.M.: The C₄ syndrome: a structural analysis. – *Annu. Rev. Plant Physiol.* **25**: 27-52, 1974.
- Loomis, R.S., Rabbinge, R., Ng, E.: Explanatory models in crop physiology. – *Annu. Rev. Plant Physiol.* **30**: 339-367, 1979.
- Lopez, Y., Velez, W., El-Sharkawy, M., Mayer, J.E.: Biochemical characterization of PEPC from cassava: a preliminary report. – In: Roca, W.M., Thro, A.M. (ed.): *Proceedings of the First International Scientific Meeting of the Cassava Biotechnology Network*. Pp. 340-343. Centro Internacional de Agricultura Tropical, Cali 1993.
- MacDermitt, D.K., Loomis, R.S.: Elemental composition of biomass and its relation to energy content, growth efficiency, and growth yield. – *Ann. Bot.* **48**: 275-290, 1981.
- Mathews, R.B.: Modelling phosphorus dynamics of cassava-based agroforestry systems – Final report, R6348 sub-contract. Sisloe, Bedfordshire, MD45 4DT UK, 1998.
- Mathews, R.B., Hunt, L.A.: GUMCAS: a model describing the growth of cassava (*Manihot esculenta* Crantz). – *Field Crops Res.* **36**: 69-84, 1994.
- McCree, K.J.: Equations for the rate of dark respiration of white clover and grain sorghum, as functions of dry weight, photosynthetic rate, and temperature. – *Crop Sci.* **14**: 509-514, 1974.
- McKinion, J.M., Baker, D.N., Hesketh, J.D., Jones, J.W.: SIMCOT II: A simulation of cotton growth and yield. – In: *Computer Simulation of a Cotton Production System. Users Manual*. Pp. 27-82. Agr. Res. Serv., US Dep. Agr. 1975.
- McKinion, J.M., Baker, D.N., Whisler, F.D., Lambert, J.R.: Application of GOSSYM/COMAX system to cotton crop management. – *Agr. Syst.* **31**: 55-65, 1989.
- Mishoe, J.W., Jones, J.W., Swaney, D.P., Wilkerson, G.G.: Using crop and pest models for management applications. – *Agr. Syst.* **15**: 153-170, 1984.
- Monsi, M., Saeki, T.: Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. – *Jap. J. Bot.* **14**: 22-52, 1953.
- Monteith, J.L.: The quest for balance in crop modeling. – *Agron. J.* **88**: 695-697, 1996.
- Muramoto, H., Hesketh, J., El-Sharkawy, M.: Relationships among rate of leaf area development, photosynthetic rate, and rate of dry matter production among American cultivated cottons and other species. – *Crop Sci.* **5**: 163-166, 1965.
- Neales, T.F., Incoll, L.D.: The control of leaf photosynthesis

- rate by the level of assimilate concentration in the leaf: a review of the hypothesis. – *Bot. Rev.* **34**: 107-125, 1968.
- Ng, E., Loomis, R.S.: Simulation of Growth and Yield of the Potato Crop. – PUDOC, Wageningen 1984.
- Nickel, J.L.: Low-input, environmentally sensitive technology for agriculture. Grant F. Walton International Lecture presented at Rutgers, The State University of New Jersey. 16 October 1984. – Centro Internacional de Agricultura Tropical, Cali 1987.
- Nickel, J.L.: Research Management for Development – Open Letter to a New Agricultural Research Director. – Inter-American Institute for Cooperation on Agriculture, San Jose 1989.
- Okogbenin, E., Fregene, M.: Genetic analysis and QTL mapping of early root bulking in and F1 population of non-inbred parents in cassava (*Manihot esculenta* Crantz). – *Theor. appl. Genet.* **106**: 58-66, 2002.
- Osaki, M., Shinano, T., Yamada, M., Yamada, S.: Function of node unit in photosynthate distribution to root in higher plants. – *Photosynthetica* **42**: 123-131, 2004.
- Pan, X.: Modeling Degree Day Effects on Plant Leaf and Internode Phenological Events. – MS Thesis. Univ. Illinois, Urbana-Champaign 1997.
- Pan, X.: A Phenological Study of Pioneer hybrids. – Ph.D. Thesis. Univ. Illinois, Urbana-Champaign 2000.
- Pan, X., Hesketh, J.D., Huck, M.G.: OWSimu: An Object-oriented and Web-based Simulator for Plant Growth. – *Agr. Syst.* **63**: 33-47, 2000.
- Passioura, J.B.: Simulation models: science, snake oil, education or engineering? – *Agron. J.* **88**: 690-694, 1996.
- Peart, R.M., Curry, D.B. (ed.): Agricultural System Modeling and Simulation. – Marcel Dekker, Washington 1997.
- Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to phosphorus fertilization. I. Yield, biomass and gas exchange. – *Field Crops Res.* **35**: 1-11, 1993a.
- Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to phosphorus fertilization. II. Phosphorus uptake and use efficiency. – *Field Crops Res.* **35**: 13-20, 1993b.
- Pellet, D., El-Sharkawy, M.A.: Sink source relations in cassava: effects of reciprocal grafting on yield and leaf photosynthesis. – *Exp. Agr.* **30**: 359-367, 1994.
- Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to fertilization: growth dynamics and its implications for cropping sustainability. – *Exp. Agr.* **33**: 353-365, 1997.
- Penning de Vries, F.W.T.: The cost of maintenance processes in plant cells. – *Ann. Bot.* **39**: 77-92, 1975.
- Penning de Vries, F.W.T., Brunsting, A.B., van Laar, H.H.: Products, requirements and efficiency of biological synthesis, a quantitative approach. – *J. theor. Biol.* **45**: 339-377, 1974.
- Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M., Bakema, A.: Simulation of Ecophysiological Processes of Growth in Several Annual Crops. – PUDOC, Wageningen 1989.
- Pettigrew, W.T.: Moisture deficit effects on cotton lint yield, yield components, and boll distribution. – *Agron. J.* **96**: 377-383, 2004a.
- Pettigrew, W.T.: Physiological consequences of moisture deficit stress in cotton. – *Crop Sci.* **44**: 1265-1272, 2004b.
- Poluektov, R.A., Topaj, A.G.: Crop modeling: nostalgia about present or reminiscence about future. – *Agron. J.* **93**: 653-659, 2001.
- Portis, A.R., Jr., Salvucci, M.E.: The discovery of Rubisco activase – yet another story of serendipity. – *Photosynth. Res.* **73**: 257-264, 2002.
- Porto, M.C.M.: Physiological Mechanisms of Drought Tolerance in Cassava (*Manihot esculenta* Crantz). – Ph.D. Thesis. University of Arizona, Tucson 1983.
- Radin, J.W., Kimball, B.A., Hendrix, D.L., Mauney, J.R.: Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. – *Photosynth. Res.* **12**: 191-203, 1987.
- Raghavendra, A.S., Sane, P.V., Mohanty, P.: Photosynthesis research in India: transition from yield physiology into molecular biology. – *Photosynth. Res.* **76**: 435-450, 2003.
- Ramanujam, T.: Effect of moisture stress on photosynthesis and productivity of cassava. – *Photosynthetica* **24**: 217-224, 1990.
- Reddy, K.R., Hodges, H.F., McKinion, J.M.: Modeling temperature effects on cotton internode and leaf growth. – *Crop Sci.* **37**: 503-509, 1997.
- Ritchie, J.T.: A user-oriented model of the soil water balance in wheat. – In: Day, W., Atkin, R.K. (ed.): *Wheat Growth and Modeling*. Pp. 293-305. Plenum Press, New York 1985.
- Ritchie, J.T., Godwin, D.C., Otter-Nacke, S.J.: CERES-Wheat: A User-Oriented Wheat Yield Model. Preliminary Document. – Michigan State Univ., West Lansing 1985a.
- Ritchie, J.T., Godwin, D.C., Otter-Nacke, S.J.: CERES-Wheat: A User-Oriented Wheat Yield Model. Preliminary Document. – Michigan State Univ., East Lansing 1985b.
- Ritchie, J.T., Johnson, B.S.: Soil and plant factors affecting evaporation. – In: Stewart, B.A., Nielsen, D.R. (ed.): *Irrigation of Agricultural Crops*. Pp. 363-390. ASA-CSSA-SSSA, Madison 1990.
- Rogers, A., Fischer, B.U., Bryant, J., Frehner, M., Blum, H., Raines, C.A., Long, S.P.: Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. – *Plant Physiol.* **118**: 683-689, 1998.
- Röhrig, M., Stützel, H., Alt, C.: A three-dimensional approach to modeling light interception in heterogeneous canopies. – *Agron. J.* **91**: 1024-1032, 1999.
- Russel, G., Marshall, B., Jarvis, P.G. (ed.): *Plant Canopies: Their Growth, Form and Function*. – Cambridge Univ. Press, Cambridge – New York – Port Chester – Melbourne – Sydney 1989.
- Saeki, T.: Interrelationships between leaf amount, light distribution and leaf photosynthesis in a community. – *Bot. Mag.* **73**: 5-63, 1960.
- Salem, J.: In an interview with Lord Robert May of the UK. – *Discover* 25 (Nov.): 23-24, 2004.
- Sasson, A.: *Feeding Tomorrow's World*. – United Nations Educational, Scientific and Cultural Organization (UNESCO)/CTA, Paris 1990.
- Šesták, Z. (ed.): *Photosynthesis During Leaf Development*. – Academia, Praha; Dr W. Junk Publ., Dordrecht – Boston – Lancaster 1985.
- Šesták, Z., Čatský, J., Jarvis, P.G. (ed.): *Plant Photosynthetic Production. Manual of Methods*. – Dr W. Junk Publ., The Hague 1971.
- Sharma-Natu, P., Pandurangam, V., Ghildiyal, M.C.: Photosynthetic acclimation and productivity of mungbean cultivars under elevated CO₂ concentration. – *J. Agron. Crop Sci.* **190**: 81-85, 2004.
- Sholtis, J.D., Gunderson, C.A., Norby, R.J., Tissue, D.T.: Persistent stimulation of photosynthesis by elevated CO₂ in a sweetgum (*Liquidambar styraciflua*) forest stand. – *New Phytol.* **162**: 343-354, 2004.
- Shorter, R., Lawn, R.J., Hammer, G.L.: Improving genotypic

- adaptation in crops – a role for breeders, physiologists and modellers. – *Exp. Agr.* **27**: 155-175, 1991.
- Sinclair, T.R., Seligman, N.G.: Crop modeling: from infancy to maturity. – *Agron. J.* **88**: 698-704, 1996.
- Singh, P.: Data needs for soil water balance simulation. – In: Wani, S.P., Singh, P., Pathak, P. (ed.): *Methods and Management of Data for Watershed Research*. Pp. 49-54. ICRISAT, Patancheru 1999.
- Swaney, D.P., Mishoe, J.W., Jones, J.W., Boggess, W.G.: Using crop models for management: Impact of weather characteristics on irrigation decisions in soybeans. – *Trans. ASAE* **26**: 1808-1814, 1983.
- Tenjo, F.A., Mayer, J.E., El-Sharkawy, M.: Cloning and sequence analysis of PEP-carboxylase from cassava. – In: Roca, W.M., Thro, A.M. (ed.): *Proceedings of the First International Scientific Meeting of the Cassava Biotechnology Network*. Pp. 331-334. Centro Internacional de Agricultura Tropical, Cali 1993.
- Thornley, J.H.M.: Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. – *Ann. Bot.* **81**: 421-430, 1998.
- Thornley, J.H.M.: Instantaneous canopy photosynthesis: analytical expressions for sun and shade leaves based on exponential light decay down the canopy and acclimated non-rectangular hyperbola for leaf photosynthesis. – *Ann. Bot.* **89**: 451-458, 2002.
- Thornley, J.H.M.: Acclimation of photosynthesis to light and canopy nitrogen distribution: an interpretation. – *Ann. Bot.* **93**: 473-475, 2004.
- Thornley, J.H.M., Johnson, I.R.: *Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology*. – Oxford Sci. Publ., Clarendon Press, Oxford 1990.
- Tscherning, K., Leihner, D.E., Hilger, T.H., Müller-Sämann, K.M., El-Sharkawy, M.A.: Grass barriers in cassava hillside cultivation: rooting patterns and root growth dynamics. – *Field Crops Res.* **43**: 131-140, 1995.
- Ueno, O., Agarie, S.: The intercellular distribution of glycine decarboxylase in leaves of cassava in relation to the photosynthetic mode and leaf anatomy. – *Jap. J. Crop Sci.* **66**: 268-278, 1997.
- Veltkamp, H.J.: Physiological causes of yield variation in cassava (*Manihot esculenta* Crantz). – Agricultural University Wageningen Papers 85-6. Wageningen 1985.
- Wang, J., Hesketh, J.D., Woolley, J.T.: Preexisting channels and soybean rooting patterns. – *Soil Sci.* **141**: 432-437, 1986.
- Ware, D.H., Jaiswal, P., Ni, J., Yap, I.V., Pan, X., Clark, K.Y., Teytelman, L., Schmidt, S.C., Zhao, W., Chang, K., Cartinhour, S., Stein, L.D., McCouch, S.R.: Gramene: a tool for grass genomics. – *Plant Physiol.* **130**: 1606-1613, 2002.
- Watson, D.J.: Comparative physiological studies on the growth of field crops: I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. – *Ann. Bot.* **41**: 41-76, 1947.
- Watson, D.J.: The physiological basis of variation in yield. – *Adv. Agron.* **4**: 101-145, 1952.
- Whisler, F.D., Acock, B., Baker, D.N., Fye, R.E., Hodges, H.F., Lambert, J.R., Lemmon, H.E., McKinion, J.M., Reddy, V.R.: Crop simulation models in agronomic systems. – *Adv. Agron.* **40**: 141-208, 1986.
- White, J.W., Hoogenboom, G.: Simulating effects of genes for physiological traits in a process-oriented crop model. – *Agron. J.* **88**: 416-422, 1996.
- White, J.W., Hoogenboom, G., Jones, J.W., Boote, K.J.: Evaluation of dry bean model BEANGRO V 1.01 for crop production research in a tropical environment. – *Exp. Agr.* **31**: 241-254, 1995.
- Wortman, S., Cummings, R.W., Jr.: *To Feed This World: The Challenge and the Strategy*. – Johns Hopkins University Press, Baltimore 1978.
- Xu, D.Q., Gifford, R.M., Chow, W.S.: Photosynthetic acclimation in pea and soybean to high atmospheric CO₂ partial pressure. – *Plant Physiol.* **106**: 661-671, 1994.
- Zhang, L.X., Qi, W., Su, L., Whisler, F.: Deltasoy – an internet based database system for soybean research and production. – *Agron. J.* **94**: 1163-1171, 2002.
- Zhang, L.X., Wang, R.F., Hesketh, J.D.: Effects of photoperiod on growth and development of soybean floral bud in different maturity. – *Agron. J.* **93**: 944-948, 2001.
- Ziska, L.H., Hogan, K.P., Smith, A.P., Drake, B.G.: Growth and photosynthesis response of nine tropical species with long-term exposure to elevated carbon dioxide. – *Oecologia* **86**: 383-389, 1991.